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# SENSILLA ON THE LARVAE OF FOUR *HYPERA* SPECIES (COLEOPTERA: CURCULIONIDAE)

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*Abstract.*—The morphology, number and distribution of the antennal, mouthpart and body sensilla of the fourth instar larva of *Hypera meles* (F.) are described and compared to those of *H. nigrirostris* (F.), *H. postica* (Gyllenhal) and *H. punctata* (F.); comparisons also are made among the first, second and third instar larvae of *H. meles.* The number and distribution of the antennal and mouthpart sensilla are very similar for the four species, and they are the same for the different larval instars of *H. meles.* Only *H. punctata* exhibits some morphological differences. The antenna has two sensilla auricillica, three sensilla basiconica and one sensillum campaniformium. Sensilla campaniformia and sensilla chaetica are found on the clypeus, labrum, mandible, stipes and prementum. Six scolopophorous sensilla are found on the mandible. Only sensilla chaetica are found on the postmentum. The epipharynx has six sensilla basiconica on the anterior edge, and 12 sensilla basiconica and two sensilla chaetica deeper in the buccal cavity. The adoral surface of the mala has 11 sensilla basiconica. Ten sensilla basiconica and two sensilla campaniformia are found on the apex of the maxillary palpus whereas eight and two of the respective sensilla are found on the apex of the labial palpus; both palpi have one sensillum digitiformium on the side of the apical segment. Two types of setae are found on the body. The first type is hair-like, resembling a sensillum chaeticum, and the second type is capitate on the first instar larva of *H. meles* but clavate on the other instars of *H. meles* and the fourth instar larvae of the other three species. The second type can be found on the prodorsum, postdorsum, and spiracular area of all segments except the prothorax. *Hypera punctata* has thinner sensilla aurillica and no trifurcate sensillum basiconicum on the antenna, a different arrangement of epipharyngeal sensilla basiconica, and eight scolopophorous sensilla in the mandible. Also, *H. punctata* has a short bifurcate sensillum chaeticum on the stipes, a shorter and thinner sensillum digitiformium on the maxillary palpus, emarginated dorsal sensilla of mala without scythe-like projections, and smooth-walled clavate body setae.

*Key Words:* Curculionidae, *Hypera* spp., larvae, morphology, sensilla, setae

Larvae of North American species of the genus *Hypera* feed mostly on plants in the legume (Fabaceae) and buckwheat (Polygonaceae) families (Titus 1911, Kissinger 1964). In the southeastern United States there are four introduced species of *Hypera* which feed on clover, *Trifolium* sp., alfalfa, *Medicago sativa* L. and sweet clover, *Melilotus* sp.: (1) clover-head weevil, *H. meles* (F.); (2) lesser clover-leaf weevil, *H. nigrirostris* (F.); (3) alfalfa weevil, *H. postica* (Gyllenhal); and (4) clover-leaf weevil, *H.*

*punctata* (F.). *Hypera meles* and *H. postica* are known to be serious pests on alfalfa and clover. The life history, biology and feeding preferences of these four *Hypera* species are summarized by Chapin and Oliver (1981 and references cited within). The larvae have distinct feeding preferences: larvae of *H. meles* and *H. nigrirostris* feed on the flowers and developing seeds, larval *H. postica* feed inside leaf buds and on leaves, and larval *H. punctata* feed on leaves. To understand their feeding preferences, we need to know the various types of cephalic sensilla that are involved in the feeding behavior and physiology. However, the morphology, number and distribution of the antennal and mouthpart sensilla which play an integral role in feeding behavior are documented only for the alfalfa weevil, *H. postica* (Bland 1983).

It is common for more than one of the four above-mentioned species to infest the same field together. The ability to differentiate the four species and their different life stages is critical for decision making in pest management. A key to the fourth instar larvae of 14 *Hypera* spp. which includes these four introduced species is available (Anderson 1948). However, the couplet that separates *H. meles* from *H. nigrirostris* depends on the color of the head capsule and the relative length of the abdominal postdorsal setae (Anderson 1948: couplet 4). These characters are hard to determine in preserved specimens.

Dyar's rule (1890) often is applied to reliably differentiate the different larval instars of these weevils (Detwiler 1923, Mailloux and Pilon 1975, Tower and Fenton 1920). The different larval instars of the four above-mentioned species have been described (Detwiler 1923, Titus 1911, Tower and Fenton 1920). However, no other definite characters are reported that would enable the differentiation of the different larval instars of the same species, except in alfalfa weevil (Gurrea-Sanz and Cano 1983).

This study provides information on (1) the morphology, number, and distribution of the antennal and mouthpart sensilla on the fourth instar larvae of the lesser cloverleaf weevil, alfalfa weevil, and clover-leaf weevil and also those of the four larval instars of the clover-head weevil; and (2) the morphology of their body setae.

## MATERIALS AND METHODS

Laboratory-reared fourth instar larvae of *H. meles*, *H. nigrirostris*, *H. postica*, and *H. punctata* were placed in boiling water for 30 s, transferred to Perfix® overnight, rinsed five times with distilled water, sonicated in a dilute detergent solution for 2 s, and rinsed three times with distilled water; or, they were fixed in Poly/LEM with 4% Triton® X-100, sonicated in the fixative for 2 s, and rinsed five times in distilled water. The mouthparts were dissected from the head and placed in a flow-through cell that was made from size 00 BEEM® capsules and embedding bag material. Specimens were osmicated 24–48 h in 4% aqueous $OsO_4$, rinsed in distilled water, dehydrated in a graded ethanol series, and either critical point dried in $CO_2$ or air dried from pentane. Specimens were attached to aluminum stubs with double stick tape or conducting silver paint and sputter-coated with gold/palladium. They were examined with a Hitachi HHS-2R or JEOL JSM-35CF scanning electron microscope at 20 kV.

The reduced silver staining method of Schafer and Sanchez (1976) was used to demonstrate porous sensilla. Stained larval mouthparts were dehydrated in graded ethanol series, then cleared in clove oil for 3 days and rinsed for 5 min in xylene. The specimens were mounted in Permount® for examination with a compound microscope.

A modified Essig's technique (Essig 1948) was used to study body setae. Decapitated fourth instar larvae were cut open either along the horizontal or sagittal plane. They were cleared in Essig's fluid for 25 min at 50°C and then overnight at room temperature. The clearing procedure was repeated until a clear specimen was obtained. Larval skins were rinsed ten times in distilled water, dehydrated in a graded ethanol series, cleared in clove oil for 3 days and rinsed for 5 min in xylene, then mounted in Permount® and examined with a compound microscope. The nomenclature of the setae is based on the terminology of Anderson (1947) and that of the sensilla on Schneider (1964) and Snodgrass (1935). Descriptions, figures and measurements given are those of the fourth instar larva of *H. meles* unless otherwise stated.

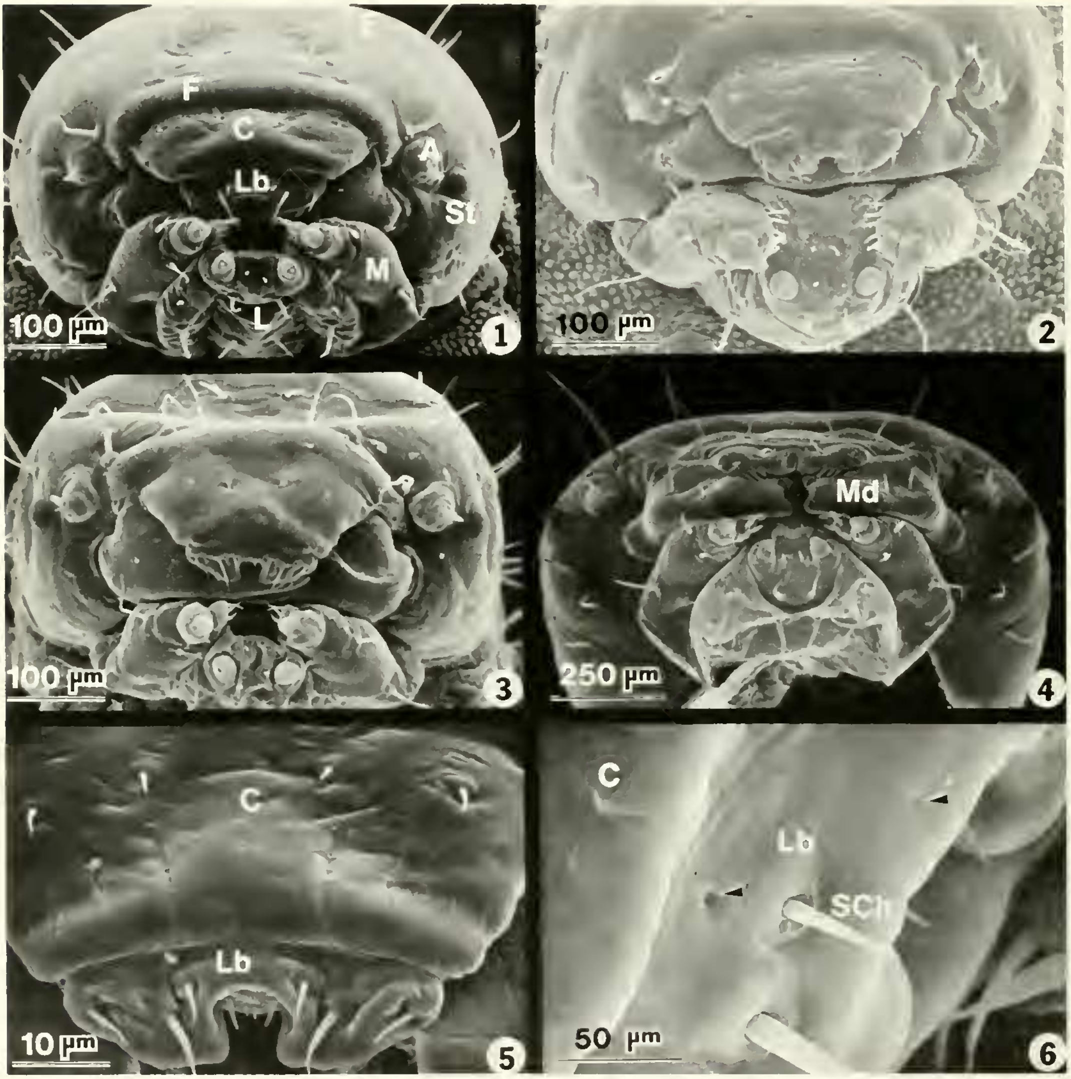
## RESULTS

The antenna and mouthparts did not differ from the published description (Anderson 1948). The former is located on the side of the epicranium between the anterior stemma and the base of the mandible. Larvae of the four *Hypera* spp. have hypognathous mouthparts, but usually the labrum is treated as the most dorsal mouthpart and the labium the most ventral. The labrum joins to the clypeus which is connected to the frons and underneath is the epipharynx. A pair of mandibles is situated behind the labrum. The ventral mouthparts consist of the labium and a pair of maxillae.

The average head capsule widths for the fourth instar larvae used in this study were 0.47 mm (n = 18) for *H. meles*, 0.39 mm (n = 3) for *H. nigrirostris*, 0.56 mm (n = 2) for *H. postica*, and 1.2 mm (n = 28) for *H. punctata* (Figs. 1–4). The average head capsule widths for the various instar larvae of *H. meles* are 0.2 mm (n = 5) for the first instar, 0.25 mm (n = 5) for the second instar and 0.33 mm (n = 5) for the third instar.

Antenna.—The antenna has seven sensilla on a short segment (Figs. 7, 8, 13, 16). The anteriorly located sensillum basiconicum is surrounded partially by three smaller sensilla basiconica, two sensilla auricillica and one sensillum campaniformium. The larger sensillum basiconicum is ca. 17 μm long, and 8 μm wide at the base where some plugged pores with diameters of ca. 400 to 600 nm are situated (Fig. 12). The outer surface of this sensillum is pitted as seen in the SEM micrographs (Fig. 9) and silver staining preparations (Fig. 7 insert). Fractured sensillum has a reticulated inner surface and the wall is ca. 0.75 to 1 μm thick (Fig. 11). Terminal pores are apparent on two of the three smaller sensilla basiconica which are ca. 2 to 3 μm long and 1 to 1.5 μm wide at the base (Fig. 10). The sensillum basiconicum between the sensilla auricillica is trifurcate and does not have a terminal pore (Fig. 14). The sensillum auricillicum is leaf-like, ca. 8 to 10 μm long, 2 μm wide at the base and constricted to ca. 1 μm halfway up the sensillum where a pore of ca. 250 nm in diameter is located (Fig. 15). It widens again towards the tip to form a blade and the widest part measures ca. 2.5 μm. On the other side of the blade there is a midrib-like structure and in some specimens the blade is emarginated. All of these sensilla lack a socket. A sensillum campaniformium, an oval depression with a raised rim of ca. 1.5 μm in diameter, is located near one of the sensillum auricillicum (Fig. 7). It often is not discernible when the cuticle is distorted during preparation. In *H. punctata* the sensillum auricillicum appears to have a narrower blade and the sensillum basiconicum between the sensilla auricillica is not trifurcate (Fig. 16).

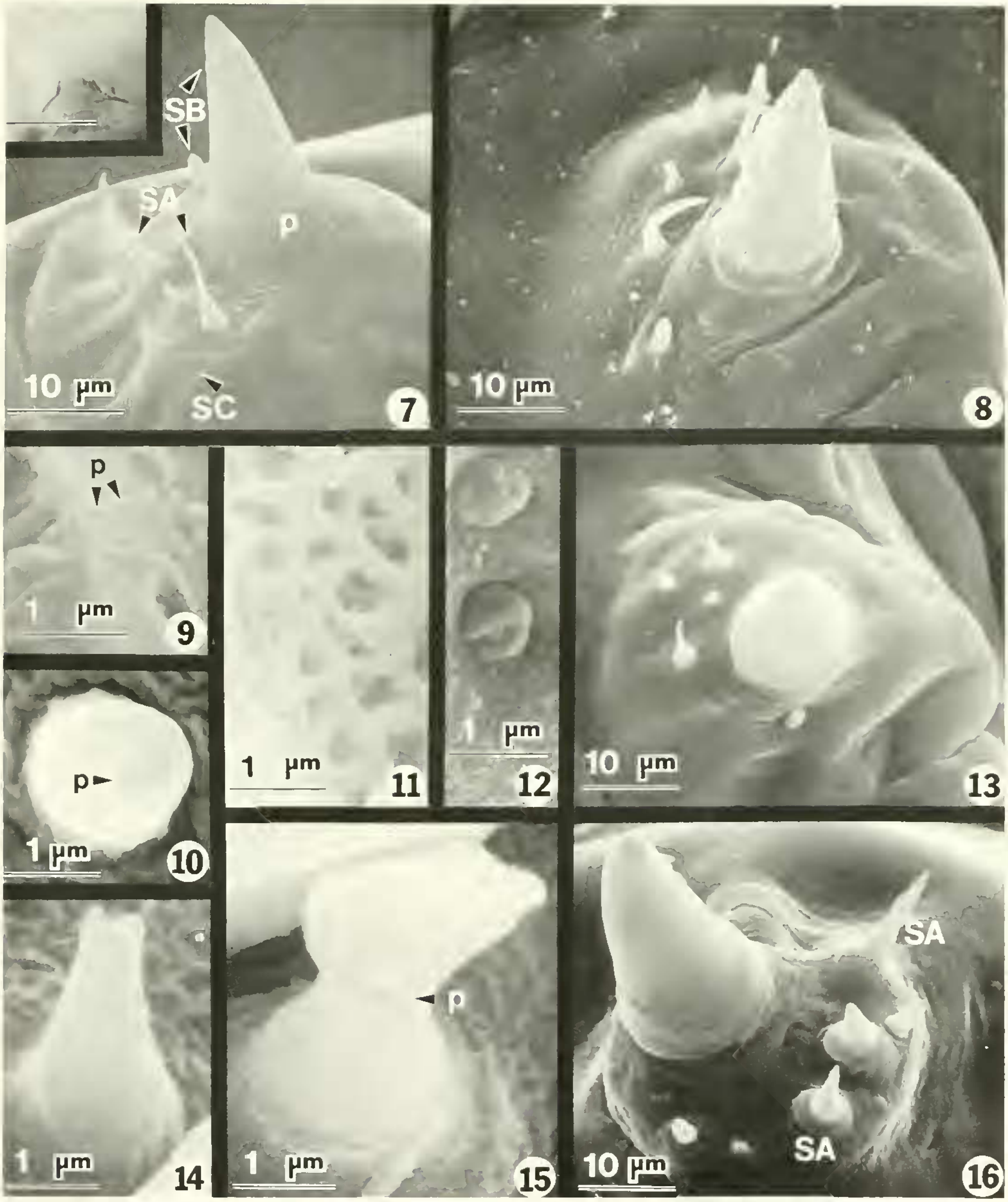
Labrum, clypeus and epipharynx.—There are three sensilla chaetica, ca. 14 to 50 μm long and 2 to 3 μm wide at the base, and one sensillum campaniformium on each side of the bilobed labrum (Figs. 1–6). Four sensilla chaetica, ca. 4 to 9 μm long and 1 to 2 μm wide at the base, are situated in the medial notch. A median sensillum campaniformium is located above the notch. Two sensilla chaetica, ca. 10 to 15 μm long and 2 to 3 μm wide at the base, are located on each side of the clypeus near the epistomal suture. One sensillum campaniformium is located between them. The sensilla chaetica are smooth-walled, attenuated, straight or slightly curved, and each has a socket. Some



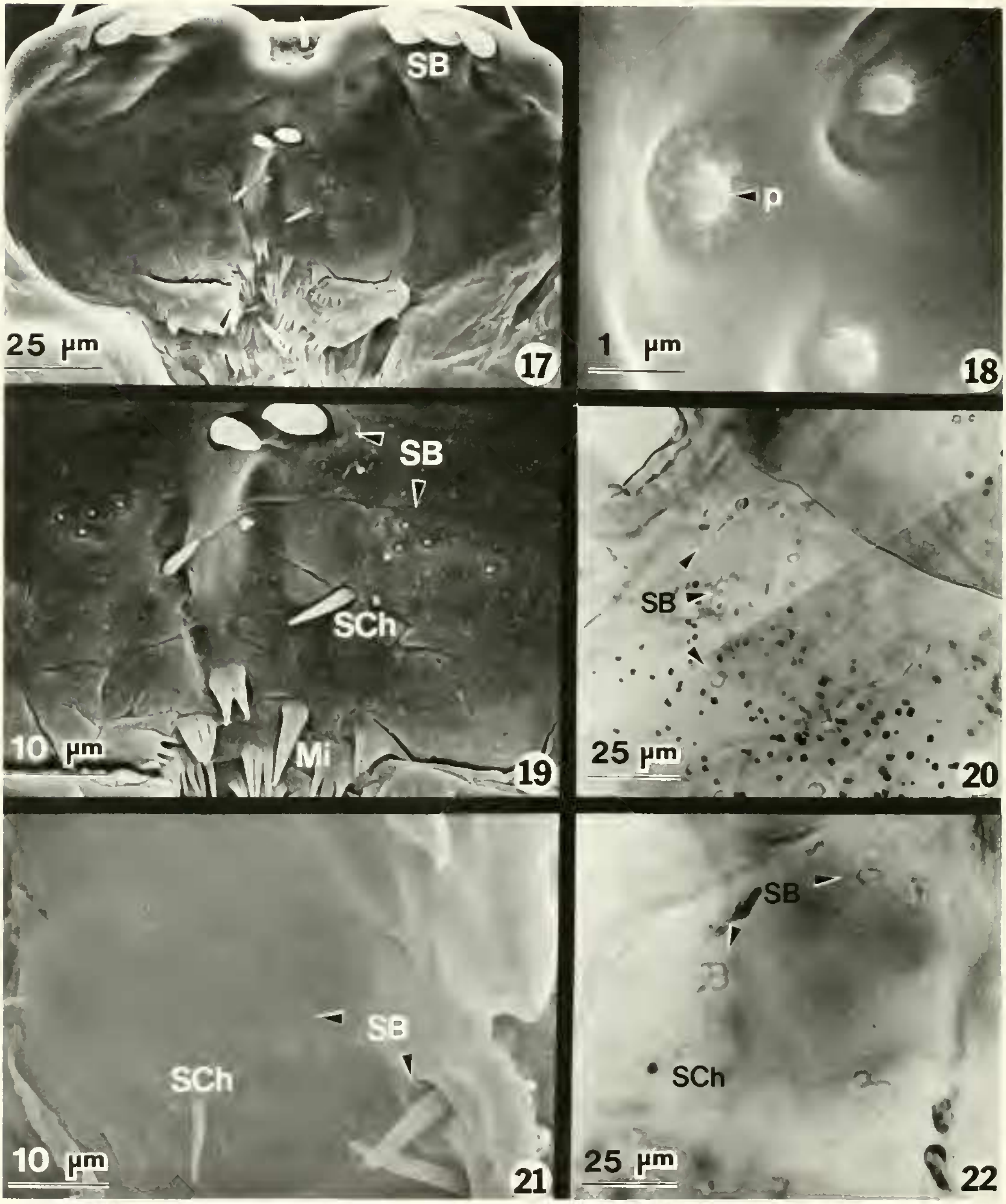
Figs. 1–6. 1–4, Head. 1, *H. meles* (frontal view). 2, *H. nigrirostris* (frontal view). 3, *H. postica* (frontal view). 4, *H. punctata* (frontal view). 5, Clypeus and labrum, *H. postica*. 6, Labrum, *H. meles*. Arrows = sensilla campaniformia.

sensilla campaniformia possess a depression of ca. 200 nm in diameter in the center.

On each side of the outer edge of the epipharynx there are three sensilla basiconica (Fig. 17). They are ca. 10 to 21 μm long and 4 to 5 μm across the widest part. These sensilla are slightly flattened, sunken and constricted at the base, and directed mesad. Deeper in the buccal cavity are 12 sensilla basiconica and two sensilla chaetica. Microtrichia are present and they are directed toward the pharynx. The two larger sensilla basiconica are ca. 10 to 12 μm long, 2 to 3 μm wide at the base and sit in a cavity (Figs. 19, 21). Their tips may be blunt or sharp. The other ten sensilla basiconica are arranged in two fields of five on each side of the midline (Fig. 17). In each field, four of the sensilla are grouped together and the other one is further away from the midline.



Figs. 7–16. Antenna. 7, *H. meles* (insert shows pitted surface of the larger sensillum basiconicum, silver staining, scale bar = 25 µm). 8, *H. nigrirostris*. 9–11, *H. meles*. 9, Larger sensillum basiconicum with pitted outer surface. 10, Sensillum basiconicum with terminal pore. 11, Fractured larger sensillum basiconicum shows reticulate inner surface. 12, Plugged pores at the base of the larger sensillum basiconicum, *H. punctata*. 13, *H. postica*. 14, Trifurcate sensillum basiconicum, *H. meles*. 15, Sensillum auricillicum shows a pore, *H. meles*. 16, *H. punctata*.



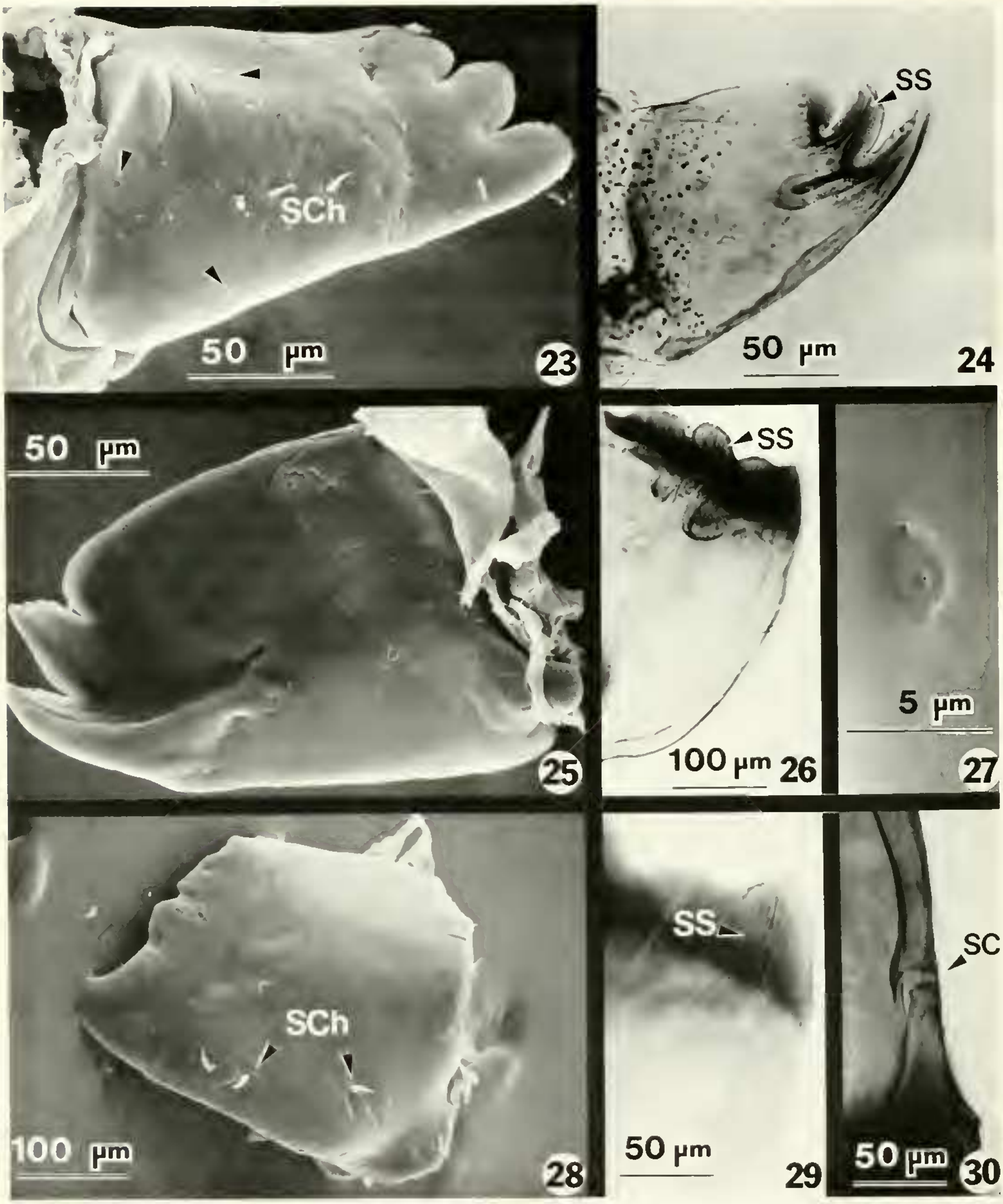
Figs. 17–22. Epipharynx. 17–19, *H. meles*. 17, Low magnification. 18, High magnification of the small sensilla basiconica. 19, Central region. 20, *H. nigrirostris*. 21, *H. postica*. 22, *H. punctata*.

The same are found in *H. nigrirostris* (Fig. 20) and *H. postica* (Fig. 21) but in *H. punctata* the five sensilla are grouped together (Fig. 22). These sensilla are short, nipple-like, ca. 300 to 400 nm wide, and sit inside an oval depression of ca. 1 µm in diameter. A pore about 100 nm in diameter, which appears plugged, is located at the tip of these sensilla basiconica (Fig. 18). Two sensilla chaetica ca. 7 μm long and 1.5 μm wide at the base, are located between these sensilla basiconica and the microtrichia (Figs. 17, 19). They are similar to the sensilla chaetica on the labrum.

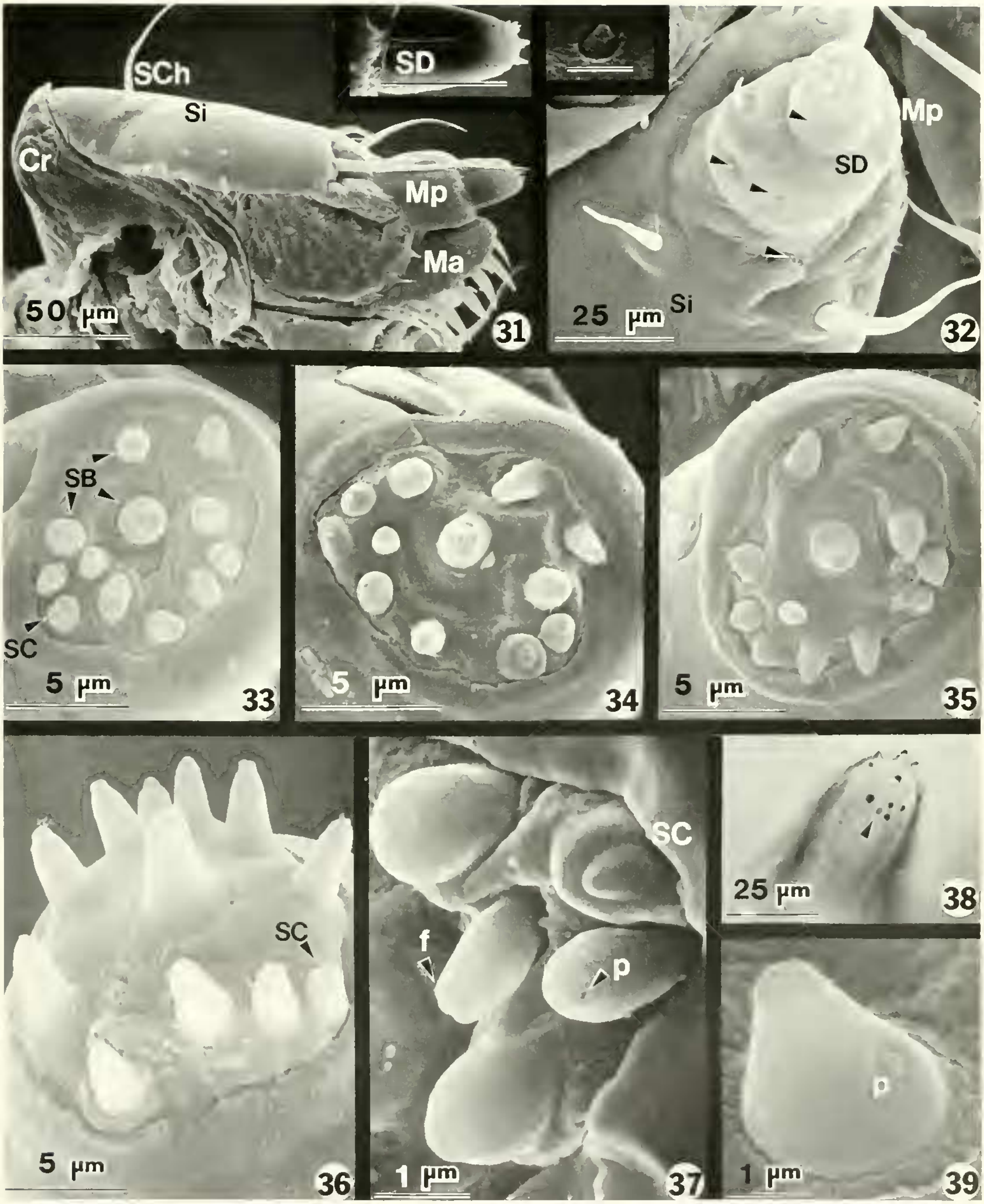
Mandible.—The anterior surface bears two sensilla chaetica which are ca. 10 μm long and 1.5 μm wide at the base (Figs. 23, 28). There are three sensilla campaniformia: one is located on the center of the dorsal surface, one on the anterior surface near the dorsal articulation and one at the boundary between the anterior and posterior surface (Fig. 23). In silver-stained preparations, the sensillum campaniformium appears as a canal in the heavily sclerotized cuticle (Fig. 30). Each mandible of *H. meles, H. nigrirostris* and *H. postica* has two apical teeth. Inside each tooth there are three scolopophorous sensilla (Fig. 24). Each mandible of *H. punctata* has four apical teeth (Fig. 28). Inside the fourth (ventral most) tooth are five scolopophorous sensilla (Fig. 29) whereas inside the second tooth there are only three (Fig. 26). The scolopophorous sensillum appears as a long canal extending from the internal cavity of the mandible into the teeth.

Maxilla.—Each maxilla consists of a fused cardo and stipes with the mala on the adoral side, and bears a two-segmented palpus on the other side (Figs. 31, 32). No sensilla are found on the cardo. The stipes has four sensilla chaetica, ca. 5 to 75 μm long and 3 to 5 μm wide at the base, and four to five sensilla campaniformia. Two longer sensilla chaetica, each accompanied by a sensillum campaniformium, are found on the aboral side of the stipes: one near the cardo and one near the palpus. Two shorter sensilla chaetica are found on the ventral surface near the palpus and the shortest one, accompanied by a sensillum campaniformium, is closer to the mala. In *H. punctata* the shortest sensillum chaeticum is bifurcate. Another sensillum campaniformium is situated on the aboral side of the articulating membrane between the palpus and the stipes. It is a short cone or dome situated in an oval depression of ca. 2 μm in diameter (Fig. 32 insert). The sensillum campaniformium located on the dorsal surface of the stipes where it joins the epicranium is found only in *H. meles* and *H. nigrirostris* but not in the other two species.

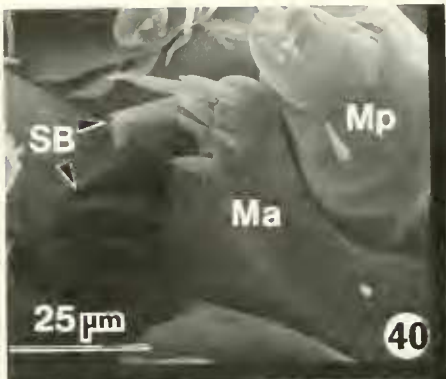
The basal segment of the palpus has one short sensillum chaeticum, ca. 3 μm long and 1.5 μm wide at the base, and two sensilla campaniformia on the ventral surface (Fig. 32). The second segment has one sensillum digitiformium on the aboral surface, one sensillum campaniformium on the ventral surface adjacent to the sensillum digitiformium and a group of 12 sensilla on the apex (Figs. 32–36). The sensillum digitiformium is ca. 12 μm long, 3 μm wide, rod-shaped, smooth-walled, socketed and lies in a groove. In some preparations a pore can be found on the distal tip. In *H. punctata*, the sensillum digitiformium is much shorter and thinner when compared to the size of the second palpal segment (Fig. 31 insert) whereas in the other three species it is almost as long as the second palpal segment (Fig. 32). The 12 sensilla on the apex consist of two sensilla campaniformia and ten sensilla basiconica. The sensillum campaniformium is a short cone ca. 500 nm in diameter and sits in an oval depression of ca. 700 nm in diameter on an elevated base. The rim of the depression is lower on the outer edge thus exposing the cone. One sensillum campaniformium is found facing the ventral surface and the other facing the adoral surface (Figs. 33–36). The sensilla basiconica are ca. 1.5 to 2 μm high and 0.5 to 2 μm wide at the base, cone to peg-like, and without a socket. In some of the sensilla basiconica, the terminal pore is surrounded by a lip and in the others by finger-like projections (Fig. 37). The centrally located sensillum basiconicum is larger than the rest and only lightly stained by silver just below the tip, whereas the other sensilla basiconica were deeply stained (Fig. 38). It does not



Figs. 23–30. Mandible. 23, Anterior and dorsal surface, *H. meles*. Arrows = sensilla campaniformia. 24, Scolopophorous sensilla, *H. nigrirostris*. 25, Posterior surface, *H. postica*. 26, Scolopophorous sensilla, *H. punctata*. 27, Sensillum campaniformium, *H. meles*. 28, Anterior surface, *H. punctata*. 29, High magnification of scolopophorous sensilla, *H. punctata*. Note only four of the five sensilla are visible. 30, Sensillum campaniformium at the boundary between the anterior and posterior surface, silver staining, *H. punctata*.



Figs. 31–39. Maxilla. 31, Dorsal view, *H. meles* (insert shows the distal palpal segment, *H. punctata*, scale bar = 50 µm). 32, Anterior-ventral view of the palpus, *H. meles* (insert shows sensillum campaniformium at the junction of the palpus and stipes, scale bar = 2.5 µm). 33–39, Apex of the palpus. 33, *H. meles*. 34, *H. nigrirostris*. 35, *H. postica*. 36, *H. punctata*. 37, High magnification of sensilla basiconica and sensillum campaniformium on the ventral region, *H. meles*. 38, Sensilla basiconica stained at the tips, silver staining, *H. punctata*. Note sensillum campaniformium is not stained (arrow). 39, Larger sensillum basiconicum with a plugged pore near the base, *H. postica*.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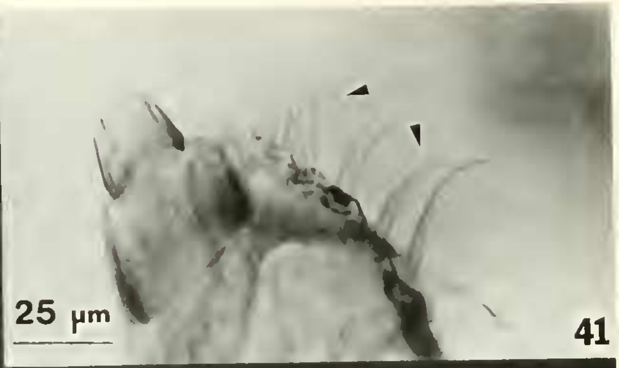
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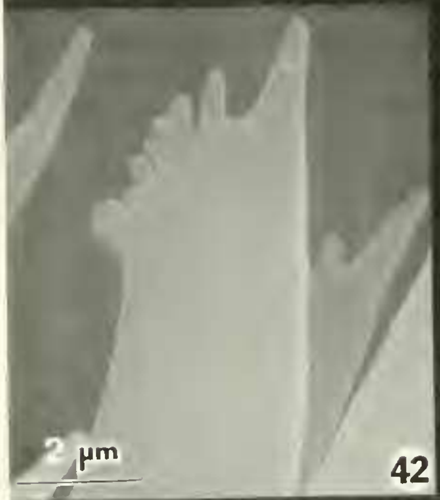
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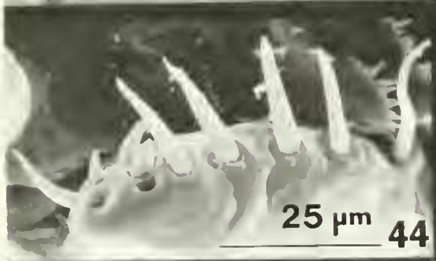
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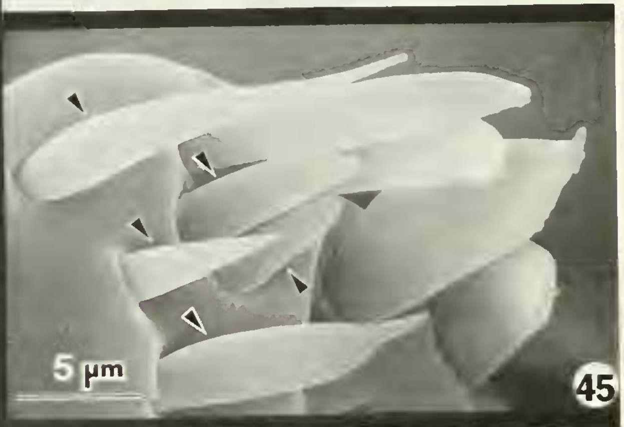
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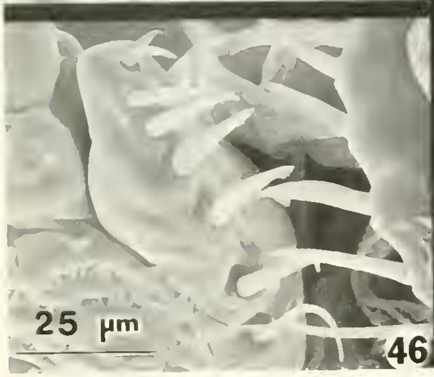
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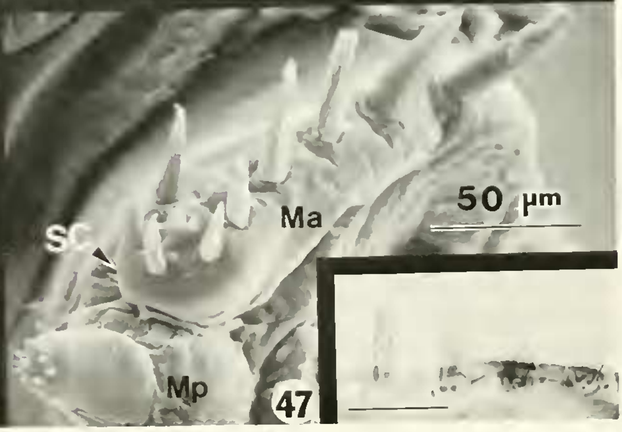
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appear to have a terminal pore. However, a plugged pore which is ca. 300 nm in diameter, is found at the base of this sensillum (Fig. 39). It may be the ecdysial pore.

The adoral surface of the mala bears 11 sensilla and the ventral surface bears only one sensillum campaniformium near the apex (Fig. 47). Along the dorsal margin of the adoral surface extending into the buccal cavity are six sensilla basiconica, whereas in the central region and along the ventral margin of the distal adoral surface, there are five sensilla basiconica (Figs. 40–47). These 11 sensilla project mesad. Anderson (1947) called them the dorsal and ventral setae of mala, respectively. These sensilla range from ca. 6 to 37 μm long, and ca. 2 to 3 μm wide at the base. In *H. meles, H. nigrirostris* and *H. postica,* they have a smooth wall and some of the dorsal sensilla of mala bear irregular scythe-like projections at the tip (Fig. 42). In *H. punctata,* these sensilla measure ca. 6 to 48 μm long, and ca. 3 to 11 μm wide at the base and possess emarginated walls. Their tips are rough and have no scythe-like projections (Fig. 47). In optical sections of the silver staining preparation these sensilla appear to have a thick wall (Fig. 47 insert). In all four species these malar sensilla have sockets. A terminal pore is apparent on the two shorter medial ventral sensilla of mala (Fig. 45) and they were stained by silver at the tips (Fig. 43).

Labium.—The labium consists of the prementum and the postmentum separated by the premental sclerite. A pair of one-segmented labial palpi is situated on each side of the prementum. There are one pair of sensilla chaetica, ca. 10 μm long and 2.5 μm wide at the base, and one pair of sensilla campaniformia, ca. 2.5 μm in diameter, on the prementum near the edge of the buccal cavity (Figs. 48, 49). Another pair of similar sensilla chaetica and sensilla campaniformia are located between the palpi, and a third pair of sensilla chaetica which are approximately three times as long are near the premental sclerite. One sensillum campaniformium is found on the base of the aboral side of the palpus (Fig. 49). Posterior to this, on each side of the premental sclerite one short sensillum chaeticum which is ca. 2.5 μm long and 1.5 μm wide at the base, is found adjacent to the postmentum and also accompanied by a sensillum campaniformium (Fig. 49). Both sensilla campaniformia are ca. 1 to 1.5 μm in diameter. The former is dome-shaped, whereas the latter is crateriform. The palpus has one sensillum digitiformium on the dorsal surface (Fig. 56), two sensilla campaniformia on the ventral surface (Fig. 52), and a group of ten sensilla on the apex (Fig. 48). Unlike the sensillum digitiformium on the maxillary palpus, this one is wider than long, measures ca. 2 μm long and 3 μm wide, and does not seem to have a socket (Fig. 57). Although the number of sensilla is different from the apex of the maxillary palpus, the spatial arrangement and morphology of the sensilla are very similar. Seven sensilla basiconica and two sensilla campaniformia partially surround a central larger sensillum basiconicum (Figs. 50, 51, 53, 54, 55).

There are three pairs of sensilla chaetica on the postmentum. Two of these are situated laterally and one pair medially. The anterior-most pair is the shortest, ca. 15 μm long and 2 μm wide at the base. The pair adjacent to them is the longest, ca. 40 μm long and 6 μm wide at the base. The medial pair are ca. 24 μm long and 4 μm wide at

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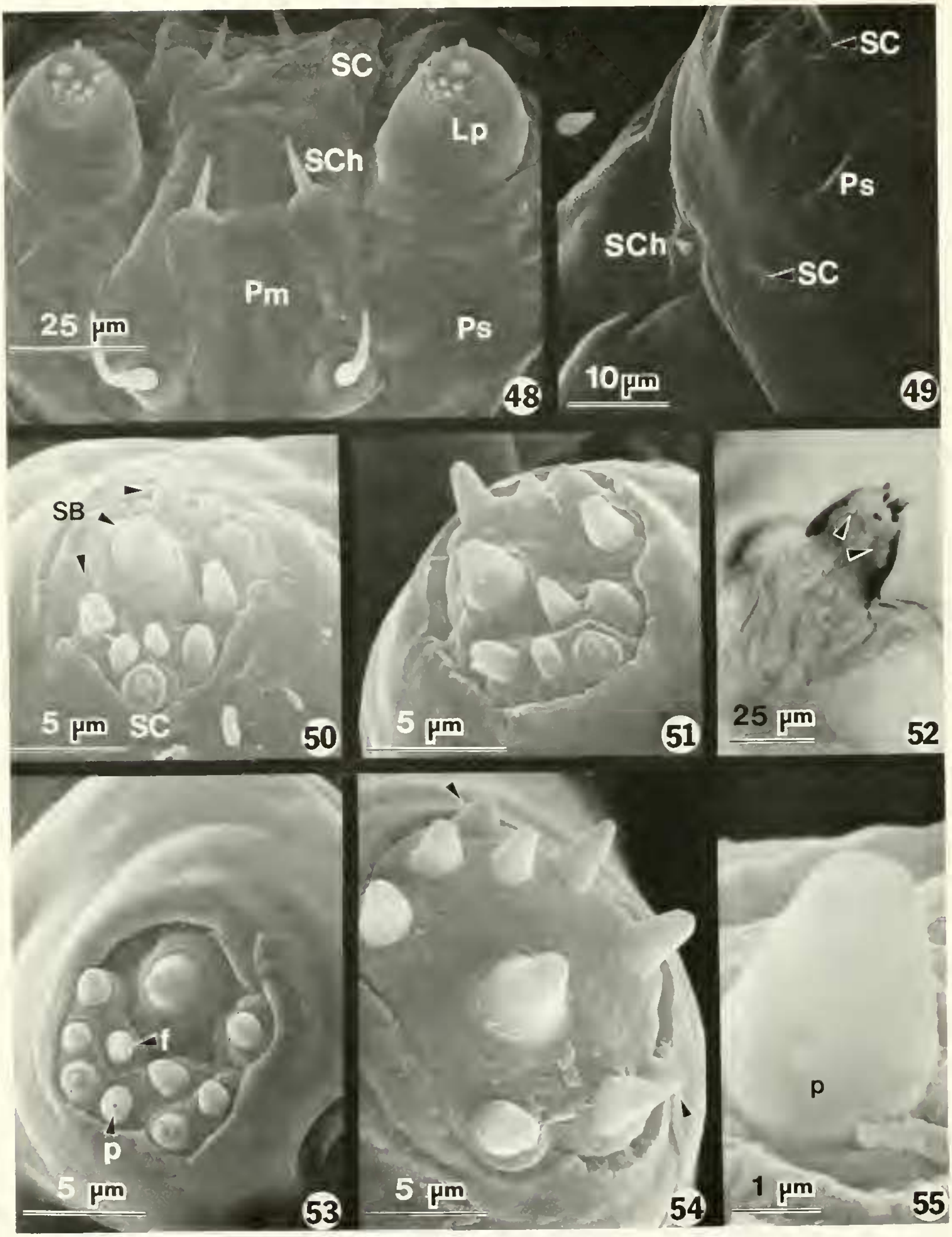
Figs. 40–47. Mala. 40–43, *H. meles.* 40, Mala (ventral view). 41, Dorsal sensilla of mala (arrows), silver staining. 42, High magnification of dorsal sensilla of mala. 43, Medial ventral sensilla of mala, silver staining. Arrow indicates stained tip. 44, *H. nigrirostris.* 45, Ventral sensilla of mala (arrows), *H. meles.* Note the position of the two medial sensilla as compared with Fig. 43. 46, *H. postica.* 47, *H. punctata* (insert shows the thick-walled dorsal sensilla of mala, silver staining, scale bar = 50 μm).



Figs. 48–55. 48, Prementum, *H. meles*. 49, Premental sclerite, *H. meles*. 50–55, Labial palpus. 50, Apex, *H. meles*. 51, Apex, *H. nigrirostris*. 52, Sensilla campaniformia on the ventral surface (arrows), silver staining, *H. meles*. 53, Apex, *H. postica*. 54, Apex, *H. punctata*. Arrows = sensilla campaniformia. 55, Larger sensillum basiconicum on the apex with a plugged pore near the base, *H. meles*.

the base. The base of the postmentum is covered with asperites similar to those found on the body.

Body.—The number and distribution of setae on the body are the same for the fourth instar larvae of *H. meles, H. postica,* and *H. punctata.* They are similar to the description on *Pissodes strobi* (Peck) (Anderson 1947) but have more setae, ca. 10 μm long and 2 μm wide at the base (Fig. 59), in the following regions:

1. Two setae on the side between the pronotum and the epicranium.
2. Three setae on the side between the pedal area and epicranium adjacent to the postmentum.
3. Two setae on the spiracular area and one seta anterior to the pedal area of the meso- and metathorax.
4. One seta on the spiracular area of the first to the seventh abdominal segment.

Moreover, the anal lobe (tenth abdominal segment) has no setae. The differences in the relative sizes of the setae are similar to those previously reported by Anderson (1948) except that the postdorsal seta 2 of *H. postica* on the fifth and sixth abdominal segments is clavate instead of attenuate (Anderson 1948: figs. 20, 21).

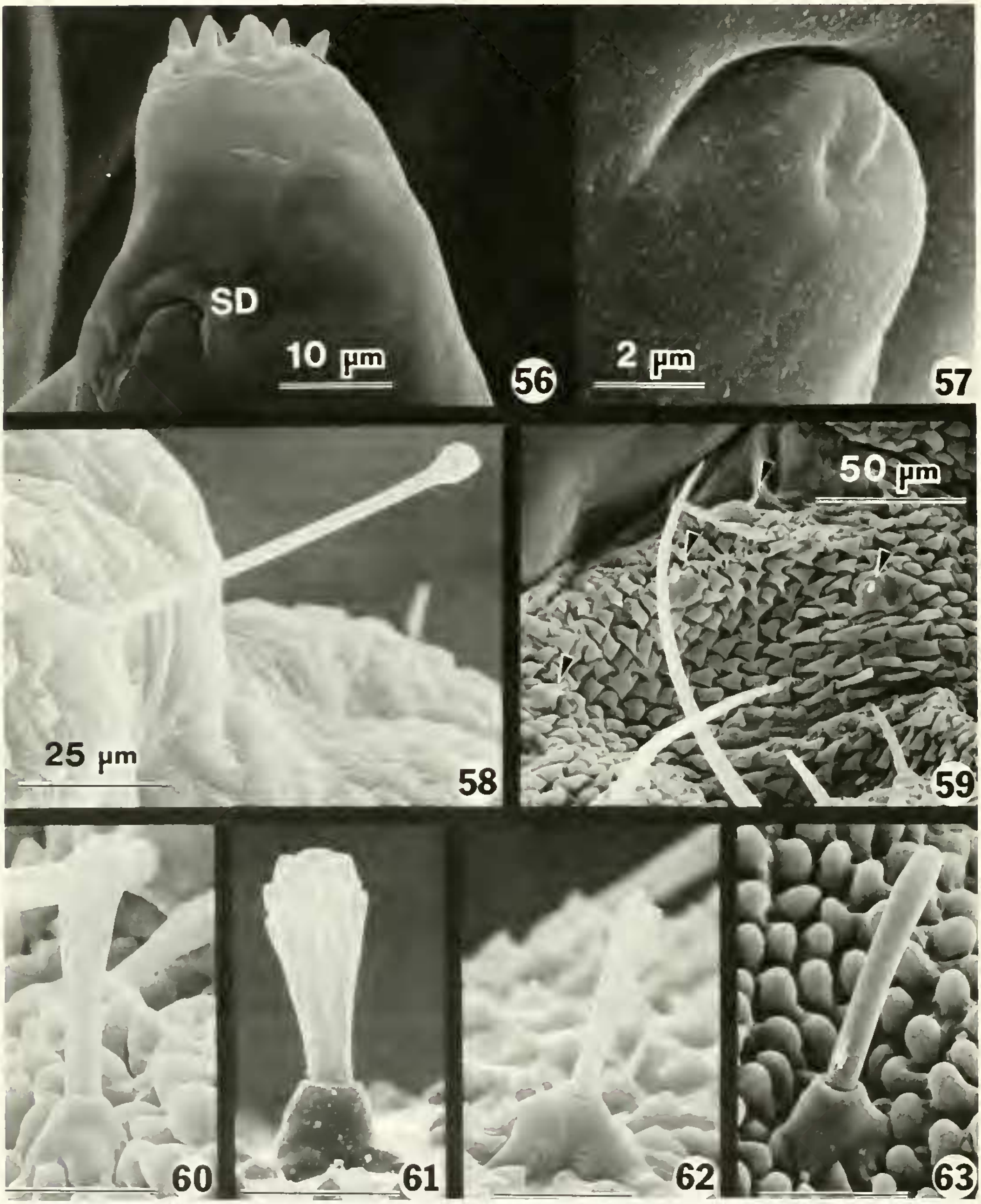
In *H. meles* two morphological types of setae are present on the body. The first type is smooth-walled and resembles a sensillum chaeticum. It is straight or slightly curved and varies from ca. 10 to 200 μm long and 2 to 7 μm wide at the base (Fig. 59). The second type is clavate and can be found on the prodorsum, postdorsum and spiracular area of all segments except the prothorax. Both types of setae have sockets. A unique variation of the second type is found in the first instar larva. It is capitate, smooth-walled, ca. 70 to 230 μm long, 3 to 8 μm wide at the base and the distal bulb is ca. 7 to 10 μm in diameter (Fig. 58). The longer ones are found on the last three abdominal segments. In later instars, clavate setae have overlapping plates on the distal end and a smooth middle piece (Figs. 60–62). On the last three abdominal segments, some of the clavate setae are replaced by long sensilla chaetica-like setae which are ca. 160 μm long and 8 μm wide at the base.

The first type of setae is found on all four *Hypera* spp. The clavate seta has the same appearance in *H. nigrirostris* and *H. postica,* but in *H. punctata* it does not have overlapping plates and the whole seta appears smooth (Fig. 63).

## DISCUSSION

The number and distribution of the antennal and mouthpart sensilla are very similar for the four species, and they are the same for the different larval instars of *H. meles.* Only *H. punctata* exhibits some morphological differences.

The morphology, number and distribution of the antennal and mouthpart sensilla of *H. postica* reported here are different from those previously reported by Bland (1983) in the following aspects. Bland (1983) did not mention that the sensillum basiconicum (sensillum 4—Bland 1983) between the sensilla auricillica is trifurcate. In both the maxillary and labial palpi he did not mention the sensilla digitiformia and sensilla campaniformia found on the side, and called all sensilla on the apex of both palpi, sensilla basiconica. But, I suggest that the two sensilla campaniformia be named as such because they resemble those in the wireworms (Bellamy 1973, Doane and Klingler 1978), adult *Dendroctonus ponderosae* Hopkins (Whitehead 1981) and adult *Ips typographus* L. (Hallberg 1982). In the last two species tubular bodies are present in the sensilla, which suggests that they are mechanoreceptors. On some of the ventral sensilla of the mala (galea—Bland 1983) the shape of the tip is variable rather than trifurcate as reported by Bland (1983). The sensilla found in these four *Hypera* spp. also resemble those on the rice weevil larvae, *Sitophilus oryzae* (L.) in their distribution pattern. However, the latter has three to four more



Figs. 56–63. 56, Sensillum digitiformium on the dorsal surface of the labial palpus, *H. punctata.* 57, High magnification of the sensillum digitiformium similar to Fig. 56. 58, Capitate seta, first instar larva, *H. meles.* 59, Short sensilla chaetica-like setae (arrows) on the prothorax near the epicranium, *H. meles.* 60–63, Clavate seta. 60, *H. meles.* 61, *H. nigrirostris.* 62, *H. postica.* Scale bar for Figs. 61–62 = 25 μm. 63, *H. punctata.* Scale bar = 50 μm.

sensilla on the antenna, and sensilla auricillica are absent. It also has three less sensilla basiconica on both the mala and apex of the labial palp (Speirs et al. 1986).

Sensilla auricillica are common on the antennae of adult Lepidoptera. They are reported to be chemoreceptors (Flower and Helson 1974, Faucheux 1984), temperature and humidity receptors (Subchev 1980), or receptors for selecting oviposition sites (Flower and Helson 1976). These sensilla are quite variable in shape (Subchev 1980). They are perforated and different from those found in this study. On the antenna of the adult cave beetle, *Aphaenops cryticola* Linder, the sensilla auricillica which are called "sensilla basiconica inflata" are considered to be chemoreceptors (Juberthie and Mazzoud 1977). Bland (1983), however, suggested that the sensillum auricillicum in *H. postica* may be simply flattened mechanoreceptors.

The pitted surface and the reticulate inner wall structure suggest that the larger sensillum basiconicum of the antenna is a single-walled, multiporous sensillum. This is similar to the "lobe membraneux" of *Speophyes lucidulus* Delar larva (Corbiere 1969) and the antennal sensory appendix of *Ctenicera destructor* (Brown) larva (Scott and Zacharuk 1971). Plugged pores on the base of the antennal sensory cone of *Aedes aegypti* (L.) larva, which serve as attachments of dendritic sheath (Zacharuk et al. 1971), are also found on these four *Hypera* spp.

The sensilla basiconica on the apex of the maxillary and labial palpi are believed to be multiporous because they are only stained slightly on the tip by the silver stain and a terminal pore is not apparent. The presence of plugged (ecdysial) pores at the base may indicate the possibility of absence of a terminal pore (Zacharuk 1980). In adult *Ips typographus,* single-walled sensilla that occur on the maxillary and labial palpi which have a system of pores penetrating the apex, are considered to be both gustatory and olfactory in function (Hallberg 1982). Thermoreceptor cells are known to bind to multiporous double-walled chemoreceptors in *Periplaneta americana* (L.) (Altner et al. 1977). The function of these sensilla basiconica found in this study may be primarily olfactory.

The sensilla basiconica on the antenna, epipharynx, mala, maxillary and labial palpi, which possess a terminal pore (uniporous) may serve as gustatory receptors (Zacharuk 1980). They can also be bimodal, both mechanoreceptor and gustatory receptor, like the lateral sensillum of the galea in larval *Entomoscelis americana* Brown (Mitchell 1978, Mitchell et al. 1979), uniporous pegs of the maxilla and labium in adult *Dendroctonus ponderosae* (Whitehead 1981) and the terminal pore sensilla in adult *Ips typographus* (Hallberg 1982). The lip and finger-like projections around the pore may regulate the pore opening to expose the dendrites to or conceal them from stimulants (Blaney and Chapman 1969). The nipple-like sensilla basiconica on the epipharynx of *Ctenicera destructor* larva are also found as two groups of five sensilla in which Zacharuk (1962) termed the 'oral plate organ' and suggested that they were gustatory receptors.

The trifurcate sensillum basiconicum found on the antenna, the six sensilla basiconica found on the anterior edge of the epipharynx, the pair of sensilla basiconica found in front of the nipple-like sensilla basiconica on the epipharynx, and the dorsal sensilla of mala, exept the medial two, do not possess a terminal pore and their lumens do not pick up the silver stain. In the colorado potato beetle larvae, *Leptinotarsa decemlineata* (Say) the longer sensilla on the edge of the galea are believed to be mechanoreceptors protecting the two central contact chemoreceptors (Mitchell and Schoonhoven 1974). Some non-porous sensilla with inflexible sockets found on the antenna of *Locusta migratoria* (L.) (Altner et al. 1981) and *Drosophila* spp. (Altner et al. 1983), and also on the maxillary palpus of *Periplaneta americana* (Altner and Stetter 1982) are known to be thermo- and hygroreceptive. The information gathered for these sensilla basiconica in this study is not enough to ascribe a particular function.

Sensilla campaniformia and sensilla chaetica are believed to be mechanoreceptors (McIver 1975). The form of sensilla campaniformia vary from simple depressions (Fig. 27) to elaborate dome-shaped organs (Figs. 32 insert, 37). Pringle (1961) proposed that specialization of arthropod proprioceptors arose by slowly increasing restriction of conditions, such as their orientation and the thickness of their cuticle, producing the strain. This is illustrated by the sensilla campaniformia on the halteres of the muscid flies (Pringle 1948) and *Drosophila melanogaster* Meigen (Chevalier 1969). Zill and Moran (1981) found that the responses of the tibial sensilla campaniformia in *Periplaneta americana* are related to their position and cap orientation. Thus, it is possible that the simple-structured sensillum campaniformium like those on the prementum may respond to one form of cuticular stress while the more elaborate ones that are situated between the palpus and stipes may respond to another form.

In larval *Ctenicera destructor,* the sensillum digitiformium on the labial palpus is found to be responsive to mechanical stimulations (Zacharuk et al. 1977). In the maxillary palpi of *Agabas bipustulatus* (L.) and *Hydrobius fuscipes* (L.), the sensilla digitiformia are reported to be hygro- and thermoreceptor because they do not possess a special socket and tubular body, and the outer dendritic segment divides into several branches in the shaft (Guse and Honomichl 1980). However, these two kinds of sensilla only differ in morphology by the possession of a socket. It is possible that the sensilla digitiformia found in this study are mechanoreceptors.

The scolopophorous sensilla are similar to those found in larval *Speophyes* sp. (Corbiere-Tichane 1971). Zacharuk and Albert (1978) found that in elaterid larva, the scolopophorous sensillum responds electrophysiologically to an outward deformation or bending of the mandibular teeth, therefore they serve as proprioceptors monitoring the stress and deformation in biting and chewing. In *Hypera* spp. these scolopophorous sensilla probably also function similarly while the sensilla campaniformia and sensilla chaetica on the surface serve as proprioceptors and exteroceptors, respectively.

In these four *Hypera* spp. a general pattern, in which a larger sensillum basiconicum is surrounded by a group of other sensilla, is found on the antenna, and apexes of the maxillary and labial palpi, but the number of surrounding sensilla varies. The number of sensilla on the apex of the maxillary palpus is greater than the number on the apex of the labial palpus. Both conditions are true in larval *Sitophilus oryzae* (Speirs et al. 1986) and larval *Lyctus brunneus* (Stephens) (Iwata and Nishimoto 1981). In *Tribolium* spp. larvae, the apex of the maxillary palpus has one more sensillum than that of the labial palpus (Ryan and Behan 1973). The same conditions are also found in the adult *Dendroctonus ponderosae* (Whitehead 1981) and *Ips typographus* (Hallberg 1982). The functional implication of such a pattern, if there is any, is unknown.

Zacharuk (1962) reported that the number, distribution and structure of the cephalic sensilla among different genera and species of larval elaterids are very similar, and the minor differences may be related to differences in habitat. In *Tribolium* spp. larvae, Ryan and Behan (1973) found that there is no difference in number and distribution of sensilla on the last instar of two species. In this study, a similar situation is found. *Hypera punctata* is the only species among the four to show some morphological differences. The similarity in the number and distribution of antennal and mouthpart sensilla among the four *Hypera* spp. indicates that the difference in feeding preferences among the fourth instar larvae is probably due to physiological differences either at the receptor level or at the central nervous system integration level. The exact function of the sensilla can only be determined by extensive electrophysiological and ultrastructural studies. The findings of this study provide the basis for such experiments.

The capitate sensillum is also found in the first instar of *H. postica* (Bland 1983). The body setae or sensilla, including the capitate and the clavate sensilla, are believed to be mechanoreceptors. Studies on the function of larval body sensilla are scarce. Chapman (1982) in his review mentioned that Henig (1930) showed that sensilla on the thoracic tarsi of the caterpillar, *Agrochola lota* (Clerck) is equipped with a single neuron which suggests their role in mechanoreception.

In exopterygota, the number of antennal and mouthpart sensilla of different nymphal instars varies considerably as illustrated by *Periplaneta americana* (Schafer and Sanchez 1973) and *Locusta migratoria* (Chapman 1982 and references cited within). In endopterygota, these characters are not highly variable. In Coleoptera, the carnivorus larvae of *Macrodytes* spp. have more sensilla basiconica in the third instar than the first (Hamon 1961). Different instar larvae of the powder-post beetle, *Lyctus brunneus*, a xylophagous species, exhibit a difference in the shape of the apical sensilla of the maxillary palpus and in the length of the antennal segments, but there is no mention of the number of sensilla found in each larval instar (Iwata and Nishimoto 1981). Our study shows that the number of sensilla on the antenna and mouthparts of *H. meles*, a phytophagous insect, remain the same throughout larval development. This is in agreement with the similar feeding preference of the different larval instars. All larval instars feed on flowers, ovaries and developing seeds of the host (Tippins 1957).

No additional diagnostic characters were found that would enable differentiation of the fourth instar larvae of *H. meles*, *H. nigrirostris* and *H. postica*. *Hypera punctata* can be identified easily because of the larger size and number of mandibular teeth (Anderson 1948: couplet 2). Revision cannot be made at this stage. The distribution of body setae of the different larval instars may provide an alternative to using measurements of head capsule width, to differentiate the instars as was proposed for alfalfa weevil larva by Gurrea-Sanz and Cano (1983).

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### List of Abbreviations

(A) = Antenna. (C) = Clypeus. (Cr) = Cardo. (E) = Epicranium. (f) = Finger-like projections. (F) = Frons. (L) = Labium. (Lb) = Labrum. (Lp) = Labial palpus. (M) = Maxilla. (Ma) = Mala. (Md) = Mandible. (Mp) = Maxillary palpus. (p) = Pore. (Pm) = Prementum. (Ps) = Premental sclerite. (SA) = Sensillum auricillicum. (SB) = Sensillum basiconicum. (SC) = Sensillum campaniformium. (SCh) = Sensillum chaeticum. (SD) = Sensillum digitiformium. (Si) = Stipes. (SS) = Scolopophorous sensillum. (St) = Stemma.

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